

POPULATION TRENDS AND BIOLOGICAL ASPECTS OF CEREAL APHIDS (HOMOPTERA: APHIDIDAE), AND THEIR NATURAL MORTALITY FACTORS ON WINTER WHEAT IN SOUTHWESTERN IDAHO

MING-GUANG FENG,^{1,4} JAMES B. JOHNSON,^{1,5}
ROBERT M. NOWIERSKI,² AND SUSAN E. HALBERT³

Abstract.—From 1986 to 1989, winter wheat grown under irrigation in southwestern Idaho was commonly infested by five species of cereal aphids, *Diuraphis noxia* (Mordvilko), *Metopolophium dirhodum* (Walker), *Rhopalosiphum padi* (L.), *Sitobion avenae* (Fabr.), and *Schizaphis graminum* (Rondani), although their population levels differed greatly from year to year. Autoecious *S. avenae* was found overwintering on the crop and usually initiated summer infestation earlier than the other species. Heteroecious *M. dirhodum* was rarely found during the autumn and initiated summer infestations later than *S. avenae*, possibly by immigrants from its primary hosts (*Rosa* spp.). Anholocyclic *D. noxia* survived the first winter after entering the region in June 1987 and achieved a dense summer population during 1988. However, colonies were not detected after mid-December during the unusually cold winter that followed and the aphid was scarce throughout 1989. The impact of cold weather may be reduced if a holocyclic population develops as may be possible as indicated by the discovery of oviparae in Idaho (Kiriak et al. 1990). This survey yielded no evidence that nymphs or adults of *R. padi* and *S. graminum* could overwinter on the crop. Both are typically holocyclic, overwintering on chokecherry, *Prunus virginiana* L., and grasses, respectively, but can sometimes overwinter anholocyclicly (Blackman et al. 1990). The summer population levels of the whole aphid complex usually remained relatively low. The highest population levels were typically observed late in the season and were reduced by entomophthoralean fungi and/or parasitoids, thus making the use of insecticides unnecessary in most years. The length and severity of freezing periods during the winter seemed to determine the timing of population recovery or immigration, and thus population sizes, during the summer. Mycoses occurred in the first two summers, causing mortalities of 46% and 90% for *M. dirhodum* and 17% and 7% for *S. avenae*. In contrast, aphidiid parasitoids killed more *S. avenae* (35%, 81%, 4%, and 59% at peak from 1986 to 1989, respectively) than *M. dirhodum* (about 5% at peak in 1986 and 1987 only). Mortalities attributable to mycoses or parasitoids were not consistently detected for other aphid species except *D. noxia*, which suffered 1–2% parasitism during the 1988 summer. Aphid-specific predators were not abundant on winter wheat throughout the survey.

Key Words.—Insecta, cereal aphids, population dynamics, Entomophthorales, Aphidiidae, winter wheat

Small grains grown under irrigation in southwestern Idaho are infested by most species of cereal aphids that occur in North America. English grain aphid, *Sitobion avenae* (Fabr.); rose-grass aphid, *Metopolophium dirhodum* (Walker); greenbug, *Schizaphis graminum* (Rondani); bird cherry-oat aphid, *Rhopalosiphum padi* (L.); and Russian wheat aphid, *Diuraphis noxia* (Mordvilko) were most common (Feng

¹ Division of Entomology, Department of Plant, Soil and Entomological Sciences, University of Idaho, Moscow, Idaho 83843.

² Entomology Research Laboratory, Montana State University, Bozeman, Montana 59717.

³ Southwest Idaho Research and Extension Center, Parma, Idaho 83660.

⁴ Current address: Entomology Research Laboratory, Montana State University, Bozeman, Montana 59717. Permanent address: China National Rice Research Institute, Hangzhou, People's Republic of China.

⁵ From whom reprints should be requested.

1990, Johnston & Bishop 1987). *Diuraphis noxia* was first found in the area during June 1987 (Feng 1990). These aphid species are all considered to be of economic importance. Few field studies have considered the whole complex of cereal aphids. Thus, little information is available concerning the population dynamics of these aphids and their natural enemies on winter wheat from planting through harvest in North America.

In this four year field study, we investigated the population trends and biological features of several aphid species, including *D. noxia*, their fungal pathogens and their hymenopterous parasitoids in irrigated winter wheat in southwestern Idaho. Data presented in this paper provide an overview of the cereal aphid complex and should be helpful in understanding the composition and population dynamics of local cereal aphid communities, their biology, and the roles of their natural enemies.

MATERIALS AND METHODS

Field studies were conducted at or near the Southwestern Idaho Research and Extension Center in Parma, Canyon County, Idaho from 1986 to 1989. Each summer, commercial fields (5–15 ha each) were surveyed weekly from mid-May onwards; these fields were furrow-irrigated at intervals of approximately 10 days from late April or early May until crop maturity and were under regular management but with no insecticide application. Summer populations of various cereal aphids were monitored in one field in 1986, two in 1987 and 1989, and three in 1988. To observe the overwintering behavior of aphid populations on winter wheat, one early-planted (mid-September) field (about 5 ha) in Caldwell, about 30 km SE of Parma, was surveyed from the seedling stage through harvest during the 1987/88 growing season (weekly from late September through mid-November, biweekly the following month, monthly from January through mid-May, and then weekly until harvest). A second overwintering survey was conducted monthly at the same site starting in late October during the 1988/89 growing season.

Details about sample size and methods have been given elsewhere (Feng et al. 1991). Briefly, our sampling system ensured 600 tillers from 15 different locations in each field on each sampling occasion to be examined at low densities (≤ 5 aphids per tiller) and a minimum of 150 tillers at high densities (≥ 15 aphids per tiller), decreasing with increasing aphid density. Because aphid densities on winter wheat were usually low or intermediate, 300 tillers or more were sampled even at peak density.

Aphids in each sample were sorted to species and counted in situ. Records included the numbers of live aphids and those killed by mycoses (cadavers) and parasitoids (mummies). The number of tillers infested with aphids was recorded only during the last two growing seasons. Percent infestation was calculated as: $\text{infestation (\%)} = (\text{number of tillers infested} / \text{number of tillers sampled}) \times 100$. Percent mortality caused by mycoses or parasitoids was computed as: $\text{mortality (\%)} = [\text{number of cadavers (or mummies)} / (\text{sum of live aphids, cadavers, and mummies})] \times 100$.

Temperature and precipitation data from a local weather station situated at the Research and Extension Center were used to interpret the population trends and the development of aphid mycoses and parasitoids in the field.

RESULTS AND DISCUSSION

Aphid species commonly occurring on winter wheat during the survey were *D. noxia*, *M. dirhodum*, *R. padi*, *S. avenae* and *S. graminum*. Among these, *S. avenae* and *M. dirhodum* populations were more consistent than those of *S. graminum* and *R. padi* during the summers. *Diuraphis noxia* established dense populations on the 1987/88 crop, but became undetectable on winter wheat during summer 1989. Other aphid species, including *Rhopalosiphum maidis* (Fitch), *Diuraphis frequens* (Walker), and *Sipha elegans* del Guccio, were occasionally observed in small, isolated colonies and apparently were of minor economic importance.

Overwintering.—Autumn populations of *D. noxia*, *R. padi*, *S. avenae* and *S. graminum* in 1987 are shown in Fig. 1. Alatae of these four species from volunteer grain plants, corn or grasses near the field initiated infestation of winter wheat soon after seedlings emerged. No *M. dirhodum* colonies were found on winter wheat during the autumn because this heteroecious species is known to overwinter as eggs on *Rosa* spp. (Hand & Williams 1981). The densities of aphid populations and percentage of infestation both increased until mid-November. Thereafter, aphid populations were dramatically reduced (Figs. 1A, 1B) as cold temperatures ensued (Fig. 1C). Aphids became inactive or died after late December. During the following autumn and winter, only *D. noxia* and *S. graminum* were observed in the samples on 26 Oct (0.57 and 0.29 aphids per tiller, respectively) and 16 Dec (0.26 and 0.04 aphids per tiller, respectively). Thereafter, no live aphids except *D. noxia* (Fig. 1A) were detected until *S. avenae* colonies appeared in mid-May (Fig. 1B), though fundatrices of the latter species occasionally occur as early as March (S. E. Halbert, unpublished data). For convenience, the population dynamics observed in autumn and the overwintering potential of each aphid species are given separately and discussed below.

Diuraphis noxia was successful in surviving the first winter after it entered the region during the summer of 1987. The population density of this species was over one aphid per tiller during mid- to late November, with 27% of the tillers infested at peak, and remained detectable even during the coldest periods (Fig. 1A). Live aphids observed during the cold winter period consisted of older nymphs and apterae that appeared to be protected in the tightly rolled leaves. *Diuraphis noxia* dominated the complex on spring wheat during the following summer (Feng et al. 1991). However, live colonies were not found on winter wheat after late December during the colder 1988/89 winter and the aphid population did not fully recover during the following spring and summer. Live colonies were sporadic on regularly sown spring wheat (seeded in late March or early April), but were more common on late-sown spring wheat (seeded in late April or early May), after June of that year (Feng et al. 1991). There were 92 freezing days during the 1988/89 winter with a minimum daily temperature of -23°C . This contrasts to 54 freezing days with an extreme of -13°C during the 1987/88 winter and 59 freezing days with an extreme of -10°C during the 1986/87 winter (Fig. 1C). The longer duration of freezing and lower extreme temperatures appeared to contribute to the virtually undetectable levels in the *D. noxia* population on winter wheat in 1989.

Rhopalosiphum padi was one of the principal species infesting winter wheat during autumn 1987. Its population level reached 6.59 aphids per tiller (in contrast to only 1.27 for *D. noxia*) on 11 Nov and nearly half of all tillers sampled were

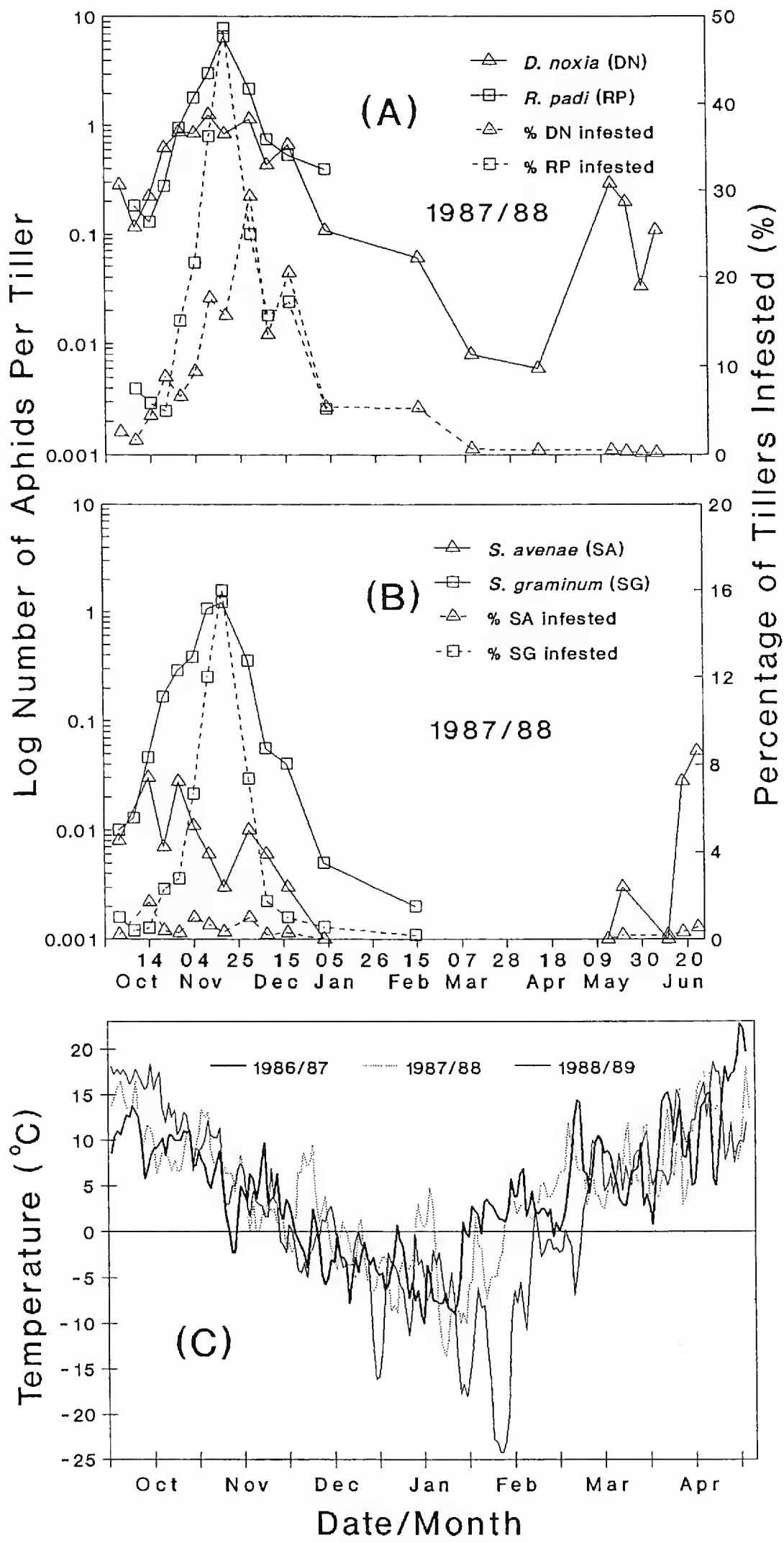


Figure 1. Autumn populations and overwintering of cereal aphids in winter wheat during the 1987/88 growing seasons. (A) *D. noxia* and *R. padi*. (B) *S. avenae* and *S. graminum*. (C) Daily mean temperature during the winter months.

infested with this species (Fig. 1A). Most colonies were found inhabiting the basal parts of plants (e.g., the undersurface of basal leaves and stems below the soil surface). Following this, *R. padi* populations rapidly decreased to 0.4 aphids per tiller (5% tillers infested) on 18 Dec. Thereafter, live aphids were not observed, though numerous dead ones (apparently having succumbed to freezing) remained visible in the field in January 1988. As a result, this species was not found during the following spring and summer. This suggests that there is little chance for *R. padi* to successfully overwinter in the parthenogenetic form on winter wheat in the study area because the 1987/88 winter was relatively mild (Fig. 1C).

As a heteroecious species, *R. padi* typically overwinters as eggs on its primary hosts, *Prunus padus* L. or related species (Robinson & Hsu 1963). Anholocyclic overwintering on winter grains or grasses is possible in mild or southern areas (Eastop 1981) (e.g., Lafayette, Indiana [Araya et al. 1987]). However, this life cycle does not occur for *R. padi* in Brookings, South Dakota (Kieckhefer et al. 1974), which is similar in latitude to southwestern Idaho. Early infestation of winter wheat followed by successful overwintering on the crop can increase losses in Washington (Pike & Schaffner 1985).

Sitobion avenae autumn populations were very small in 1987 (Fig. 1B) and undetectable in 1988. Its peak density was only 0.04 aphids per tiller, corresponding to an infestation level of less than 2% (Fig. 1B). A few oviparae were found during the autumn, but eggs were not detected. From 18 Dec onwards, live aphids were not found in the crop until mid-May of the following year.

Schizaphis graminum had a larger autumn population than *S. avenae* in 1987 (Fig. 1B). Its peak density was about one aphid per tiller (similar to the *D. noxia* population) on 18 Nov and resulted in an infestation of 16%. Thereafter, its population decreased but remained detectable until 17 Feb 1988. In contrast, during the following, colder winter, the population of *S. graminum* was detectable only until 16 Dec.

These two species are considered to be holocyclic in the northern United States (Blackman & Eastop 1984). In areas with spring and winter cereals, alatae from volunteer plants and grasses migrate to autumn-sown winter crops, on which they produce males and oviparae and then lay eggs to survive the winter months (Phillips 1916). Of the two aphid species, only *S. avenae* usually seems to fit this pattern in the study area because no sexuals of *S. graminum* were found during the survey. Although *S. graminum* survived all the periods of freezing during the 1987/88 winter (Figs. 1B, 1C), its population did not recover in the same field during the following spring and summer.

Summer Populations.—The population development of each aphid species and the mortalities caused by entomophthoralean fungi and/or aphidiid parasitoids are shown in Fig. 2 for the 1986 and 1987 summers and in Fig. 3 for the 1988 and 1989 summers. Data presented in Figs. 2 and 3 are mean estimates from two fields for 1987 and 1989 and three fields in 1988, respectively. The 1986 populations were estimated from only a single field. Aphid-specific predators such as coccinellids and syrphids were not common on winter wheat though they were sometimes abundant on spring, particularly late-sown, crops.

Initiation of Infestation.—As shown in Figs. 2 and 3, the populations of *S. avenae* were first detected on winter wheat in mid-May (1987, 1989) or late May (1986, 1988). The early colonies usually consisted of various nymphal instars and

fewer wingless adults. Thus, the starting population of this aphid species, though too small to be detected, started earlier and was possibly initiated by fundatrices that hatched from overwintered eggs, rather than by immigrants. Moreover, alate nymphs were well represented among the earliest observed nymphs, indicating a source of *S. avenae* for infesting local spring-planted grain crops. In contrast, *M. dirhodum* was found in the field one (1988), two (1986, 1987) or even three (1989) weeks later than *S. avenae*. The early colonies of *M. dirhodum*, found on plants each summer, commonly consisted of several early instars and one alate. Thus, it is postulated that the infestation of winter wheat by *M. dirhodum* was initiated by alate immigrants from its primary hosts because no colonies of this species were found during the preceding autumn.

Schizaphis graminum occurred on winter wheat at the same time as *M. dirhodum* in 1986 and 1988, but one week later in 1987 (Figs. 2 and 3). However, it was not found throughout the 1989 summer. Although *S. graminum* survived all the freezing periods during the 1987/88 winter (Figs. 1B, 1C), the population of this species was not detected until the end of the first week of June (Fig. 3A). The populations of *R. padi* were detected later than both of the above species in 1986 and a few days earlier in 1987, but were undetectable on the crop during the last two summers. Therefore, *R. padi* and *S. graminum* may have initiated their summer infestation primarily by their immigrants from other hosts or places, which is in agreement with observations from South Dakota (Kieckhefer et al. 1974).

The 1988 population level of *D. noxia* was relatively high (up to 0.16 aphids per tiller) at the first sampling time (17 May), two weeks before *S. avenae* populations were detected (Fig. 3A). Colonies of *D. noxia*, during this early period, consisted of nymphs and apterae. Therefore, it appears that 1988 summer populations of *D. noxia* on winter wheat were initiated by individuals that successfully overwintered in situ (Fig. 1A). Following the colder 1988/89 winter, initial infestation of the crop appeared to be largely due to immigration of alatae.

Population Development.—Summer populations of *S. avenae* and *M. dirhodum* were usually the highest among the aphid species found during this survey (Figs. 2 and 3). An exception occurred in 1988 when *D. noxia* populations were found to be more dense (2.99 aphids per tiller at peak) than the prior two aphid species (Fig. 3A). Though *M. dirhodum* infested the crop later than *S. avenae*, its populations peaked earlier, and were often larger, than those of *S. avenae*. The highest population densities of *M. dirhodum* and *S. avenae* were, respectively, 4.43 (25 Jun, early milky stage) and 3.73 (2 Jul, medium milky) aphids per tiller in 1986, 5.23 (3 Jul, hard dough) and 0.54 (3 Jul, hard dough) in 1987, 0.65 (21 Jun, soft dough) and 1.03 (7 Jul, nearly ripening) in 1988, and 0.46 (19 Jun, late milky) and 0.36 (26 Jun, soft dough) in 1989. Such population trends were similar to those reported by Ankersmit & Carter (1981).

The populations of *S. graminum* and, particularly, *R. padi* were relatively small and inconsistent in winter wheat during the summers. Peak densities of these two species were, respectively, 0.7 (2 Jul) and 0.03 (25 Jun) aphids per tiller in 1986, 0.6 (26 Jun) and 0.62 (3 Jul) in 1987, and 1.57 (21 Jun) in 1988 for *S. graminum* only.

These aphid species appeared to prefer different parts of the plants for feeding. *Sitobion avenae* preferred developing heads and upper leaves before heading,

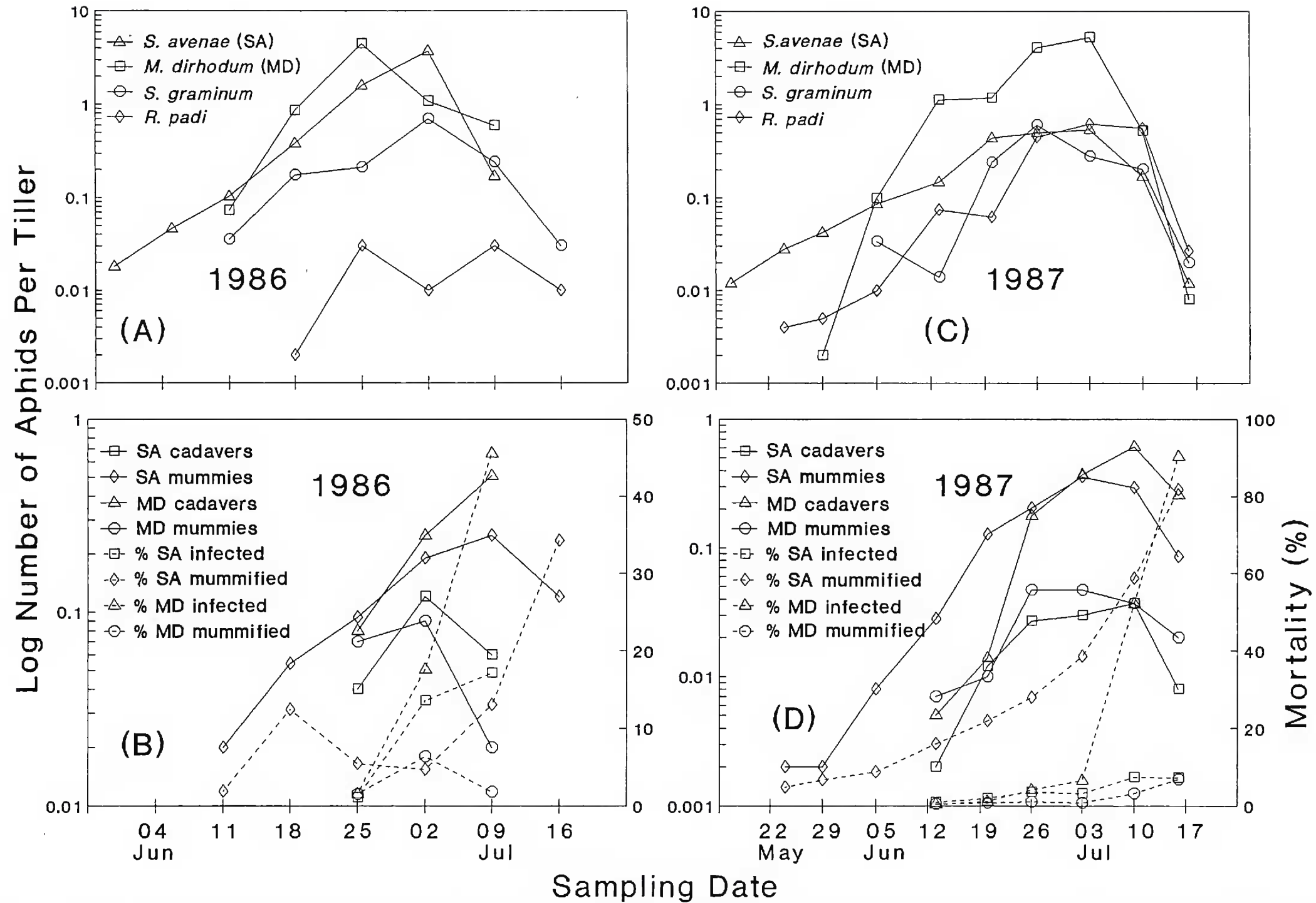


Figure 2. Summer populations of cereal aphids influenced by mycoses (cadavers) and parasitoids (mummies) in winter wheat during the 1986 (A & B) and 1987 (C & D) summers. Estimates were made from one and two fields in 1986 and 1987, respectively.

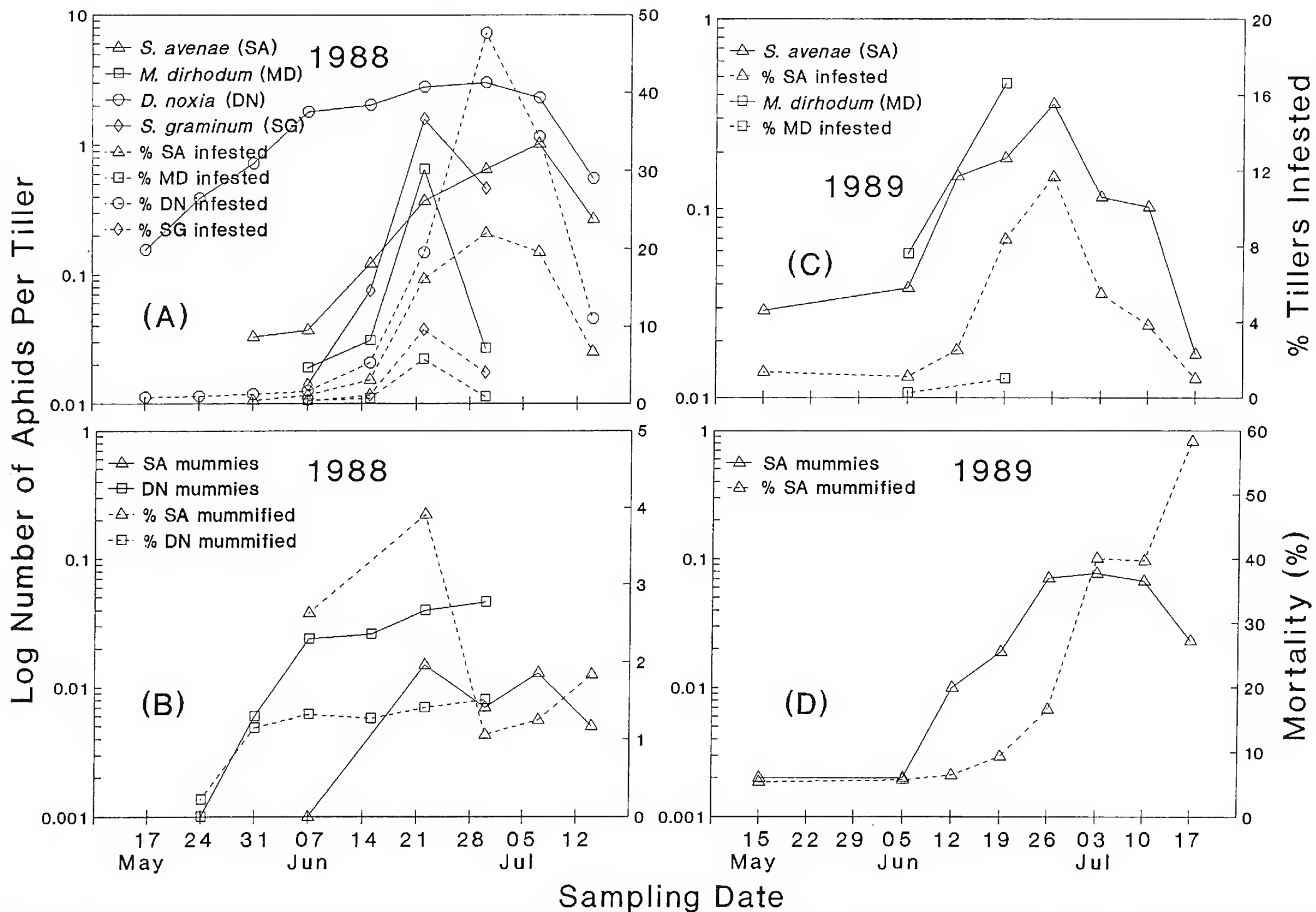


Figure 3. Summer populations of cereal aphids and their parasitoids (mummies) in winter wheat during the 1988 (A & B) and 1989 (C & D) summers. Estimates were made from three and two fields in 1988 and 1989, respectively.

whereas *M. dirhodum* tended to feed on the undersurfaces of older leaves and were rarely observed on heads. *Diuraphis noxia* preferred younger leaves, longitudinally rolled and striped when injured, at earlier stages of the crop but were also observed on heads and upper stems of more mature plants. *Schizaphis graminum* and *R. padi* were often found on leaves, on or inside the leaf sheaths and on the stems.

Mycoses.—Mycoses caused by entomophthoralean fungi appeared to significantly limit populations of *M. dirhodum* and *S. avenae* during the 1986 and 1987 summers (Fig. 2). Some cadavers of *S. graminum* and fewer of *R. padi* were also attributed to fungal infection in 1987. Few mycosed aphids of any species were found on winter wheat during the 1988 and 1989 summers (Fig. 3), although mycoses were still a principal factor reducing aphid populations in spring wheat during the same seasons (Feng et al. 1991). The highest mortalities of *M. dirhodum* and *S. avenae* in winter wheat due to fungal infection were, respectively, 46% and 17% in 1986, and 90% and 7% in 1987 (Figs. 2A, 2B). *Metopolophium dirhodum* was apparently far more susceptible to fungal infection than *S. avenae* in the field.

According to Feng et al. (1990a), the fungi capable of infecting cereal aphids on grain crops in southwestern Idaho during the 1986–1989 summers included 10 species, the most important of which was *Pandora neoaphidis* (Remaudire & Hennebert) Humber, followed by three *Conidiobolus* species. Among 2930 cadavers of six aphid species examined, 77% were killed by *P. neoaphidis* and 17.6% by *Conidiobolus* spp. Furthermore, *P. neoaphidis* and *Conidiobolus* spp. were responsible for 84% and 11% of 1417 *M. dirhodum* cadavers examined, and 24% and 68% of 217 *S. avenae* cadavers. The LC_{50} of *P. neoaphidis* for killing *M. dirhodum* was only 1.4–1.6 conidia/mm² (Feng & Johnson 1991). Thus, during the 1986–1987 summers, *P. neoaphidis* was a major pathogen associated with the mycoses of *M. dirhodum*, whereas *Conidiobolus* spp. were pathogens primarily associated with the mycoses of *S. avenae* (Feng 1991).

The patterns of aphid mycoses found in winter wheat during the survey may be interpreted as follows. First of all, having sufficient population levels of *M. dirhodum* which is more susceptible to fungal infection than some other aphid species (Feng & Johnson 1991, Feng et al. 1990b), appears to be a key factor. Mycoses occurred only during the two summers that experienced larger populations of *M. dirhodum* than *S. avenae* and other aphid species. When the *M. dirhodum* populations were small, as in 1988 and 1989, mycoses did not occur for *M. dirhodum* nor for any of the other aphid species, some of which occurred at high population levels (Fig. 3). For example, *D. noxia*, which had much higher population levels than *M. dirhodum* during the 1988 growing season, did not appear to be significantly affected by fungal infection. Second, temperature (influencing the development of both aphids and fungi) and precipitation (which increases the humidity within a crop and thus enhances conidial germination and infection) should also be considered. Cumulative precipitation and the timing of rainfall during the growing seasons greatly differed from year to year (Fig. 4B) and seemed to be more critical to the development of mycoses than temperature (Fig. 4A) (Feng et al. 1991). Frequent rainfalls throughout the 1987 summer and several small rainfalls during late June and early July in 1986 (Fig. 4B) coincided with the phase of the rapid development of mycoses in aphid populations during those summers (Fig. 2C, 2D). In contrast, there was little rain from early June

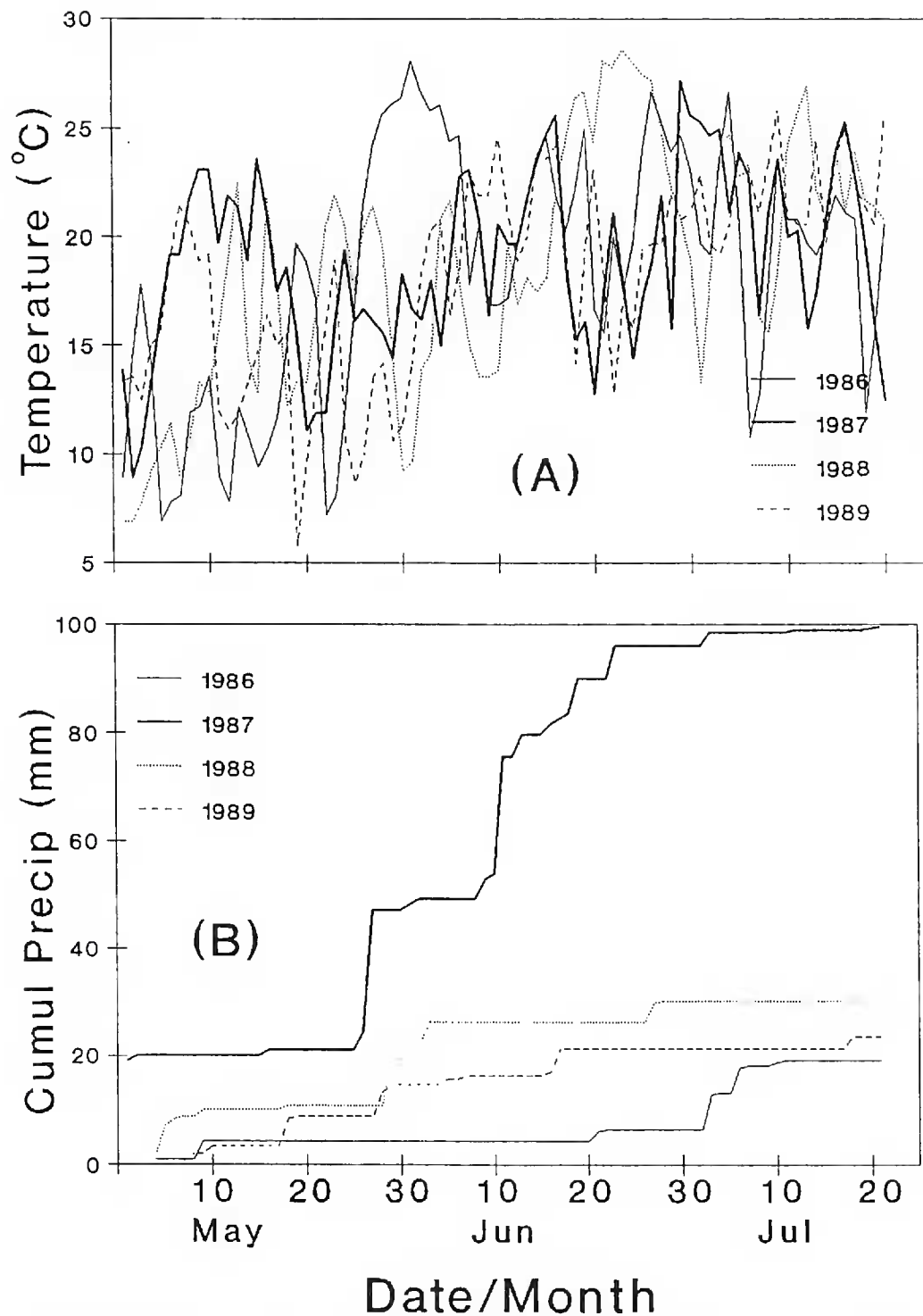


Figure 4. Weather patterns during the winter wheat growing season from 1986 to 1989. (A) Daily mean temperature ($^{\circ}\text{C}$). (B) Cumulative precipitation (mm).

through July in 1988, and no rain during the last month of the crop season in 1989 (Fig. 4B). Also, irrigation was not supplied to winter wheat from late June onwards. Thus, low moisture under the crop canopy may have contributed to the undetectable level of fungal infection in aphid populations during the last two summers.

Parasitoids.—Primary parasitoids found to attack cereal aphids on winter wheat during the survey were all aphidiids, although an aphelinid species, *Aphelinus varipes* (Foerster), may attack *D. noxia* and *S. graminum* on spring wheat and barley and *R. padi* on corn (Feng 1990). The majority of *S. avenae* and *M. dirhodum* mummies were due to parasitism by *Aphidius ervi* Haliday, but *D. noxia* mummies were mostly attributable to attack by *Diaeretiella rapae* (McIntosh). *Praon* sp., possibly *P. gallicum* Stary, was found occasionally attacking all three aphid species. Mummies of *S. graminum* and *R. padi* were infrequently found on winter wheat because of their small or inconsistent populations.

Feng et al. (1991) found that parasitoids attacked cereal aphids, particularly *S. avenae*, earlier and at lower densities than fungal pathogens (Figs. 2 and 3). Parasitism was always higher for *S. avenae* than *M. dirhodum* and appeared to be a major factor suppressing the increase of *S. avenae* populations every summer. The highest mortality due to parasitism was 35% in 1986, 81% in 1987, 4% in 1988, and 59% in 1989. However, the mortality of *M. dirhodum* due to parasitism was always found to occur at low levels (about 5% at peak), and was not detected during the 1988 and 1989 summers (Figs. 2 and 3). This indicates that parasitoids were less important than mycoses in influencing the dynamics of *M. dirhodum* populations. Similarly, *D. noxia* suffered only 1–2% mortality due to parasitoids during the 1988 summer (Fig. 3B).

General Remarks.—Based on our four year field observations, the populations of cereal aphids in southwestern Idaho were much smaller on winter wheat than on spring wheat (Feng et al. 1991). The population level of *S. avenae*, the most injurious species to developing heads (Rabbinge et al. 1981, Vickerman & Wratten 1979), achieved only about one aphid per tiller at peak density on winter wheat during the summers from 1987 to 1989 and 3.73 aphids per tiller in 1986. The populations of the less injurious species, *M. dirhodum*, were larger in the first two summers but only about five aphids per tiller at peak. The economic threshold levels for the combined populations of *S. avenae* and *M. dirhodum* are 2–4 aphids per tiller at flowering, 6–10 aphids per tiller up to milky stage, and 10 or more aphids per tiller from the milky ripe to medium-dough stage (Johnston & Bishop 1987). Therefore, the population levels of the two species observed during the survey made insecticide application unnecessary. In fact, winter wheat received no insecticide application during the growing seasons.

The population stability of *S. avenae* and *M. dirhodum* may stem from their adaptation to local weather by successfully overwintering as eggs on winter wheat and roses, respectively. This contrasts to the inconsistent populations of other aphid species. *Rhopalosiphum padi*, though not found on winter wheat during the 1988 and 1989 summers, did infest spring-planted wheat late in the seasons (from late June onwards; Feng 1990). Huge numbers of this species (up to thousands of aphids per plant) were commonly seen on corn in southwestern Idaho from late July through August or mid-September (Blackmer & Bishop 1991, Feng 1990). *Schizaphis graminum* also occurred on spring wheat after late June in 1989. These data suggest that infestation of local grain crops by *R. padi* and *S. graminum* was initiated by immigrants from other hosts. *Diuraphis noxia* appears to be able to survive local winter months with its anholocyclic life, at least in mild winters. The unusually cold 1988/89 winter was possibly a main reason that populations of *D. noxia*, *R. padi*, and *S. graminum* were undetected on winter wheat but found on other grain crops late in the following season. Therefore, the length and extremity of freezing time during winter months can apparently determine the timing of population recovery or immigration, and thus population sizes, of these aphid species during the summer.

From August through early October volunteer grains can be inhabited by numerous aphids of all the species except *M. dirhodum*, which was rarely observed after harvest (Feng 1990), and thus are sources of autumn aphid populations infesting winter wheat. However, for *R. padi* and *S. avenae*, field corn grown for

seed (plants left in the field until late September or even later after harvest) may be an even more important source of aphids to infest winter wheat (Feng 1990).

Mycoses and parasitoids are major biological mortality factors for *M. dirhodum* and *S. avenae* on winter wheat, although their influences differ from year to year. They apparently contributed to the collapse of *M. dirhodum* and *S. avenae* populations during the 1986 and 1987 summers. Even when *S. avenae* populations were small, as during the summer of 1989, there was a high level of parasitism. However, the life cycles of fungal pathogens and parasitoids associated with cereal aphids are not well understood. Cadavers were rarely found in autumn populations of cereal aphids on winter wheat. Mummies, though sometimes detected, were not common during the autumn. Their non-crop-feeding hosts are unknown in southwestern Idaho. Further study because this may help incorporate both mortality agents into a sound crop management program is warranted.

ACKNOWLEDGMENT

The authors wish to express their appreciation to K. W. Dorschner and D. J. Schotzko for critical review of this manuscript. This paper is published with the approval of the Director of the Idaho Agricultural Experiment Station as Research Paper 92703.

LITERATURE CITED

- Ankersmit, G. W. & N. Carter. 1981. Comparison of the epidemiology of *Metopolophium dirhodum* and *Sitobion avenae* on winter wheat. *Neth. J. Pl. Path.*, 87: 71–81.
- Araya, J. E., J. E. Foster & S. E. Cambron. 1987. A study of the biology of *Rhopalosiphum padi* (Homoptera: Aphididae) in winter wheat in northwestern Indiana. *Great Lakes Entomol.*, 20: 47–50.
- Blackman, R. L. & V. F. Eastop. 1984. *Aphids on the world's crops: an identification guide*. John Wiley, Chichester.
- Blackman, R. L., S. E. Halbert & T. W. Carroll. 1990. Association between karyotype and host plant in corn leaf aphid (Homoptera: Aphididae) in the northwestern United States. *Environ. Entomol.*, 19: 609–611.
- Blackmer, J. L. & G. W. Bishop. 1991. Population dynamics of *Rhopalosiphum padi* (Homoptera: Aphididae) in corn in relation to barley yellow dwarf epidemiology in southwestern Idaho. *Environ. Entomol.*, 20: 166–173.
- Eastop, V. F. 1981. The wild hosts of aphid pests. pp. 285–298. *In* Thresh, J. M. (ed.). *Pests, pathogens and vegetation*. Pitman, London.
- Feng, M. G. 1990. Fungi pathogenic to aphids (Homoptera: Aphididae) infesting irrigated grain crops in southwestern Idaho: their virulence and roles in natural control. Ph.D. Dissertation, University of Idaho, Moscow.
- Feng, M. G. & J. B. Johnson. 1991. Bioassay of four entomophthoralean fungi (Entomophthorales) against *Diuraphis noxia* and *Metopolophium dirhodum* (Homoptera: Aphididae). *Environ. Entomol.*, 20: 338–345.
- Feng, M. G., J. B. Johnson & L. P. Kish. 1990a. Survey of entomopathogenic fungi naturally infecting cereal aphids (Homoptera: Aphididae) of irrigated grain crops in southwestern Idaho. *Environ. Entomol.*, 19: 1534–1542.
- Feng, M. G., J. B. Johnson & L. P. Kish. 1990b. Virulence of *Verticillium lecanii* and an aphid-derived isolate of *Beauveria bassiana* (Fungi: Hyphomycetes) for six species of cereal aphids (Homoptera: Aphididae). *Environ. Entomol.*, 19: 815–820.
- Feng, M. G., J. B. Johnson & S. E. Halbert. 1991. Natural control of cereal aphids (Homoptera: Aphididae) by entomopathogenic fungi (Zygomycetes: Entomophthorales) and parasitoids (Hymenoptera: Braconidae and Encyrtidae) on irrigated spring wheat in southwestern Idaho. *Environ. Entomol.*, 20: 1699–1710.
- Hand, S. C. & C. T. Williams. 1981. The overwintering of the rose-grain aphid *Metopolophium*

- dirhodum* on wild roses. pp. 285–298. In Thresh, J. M. (ed.). Pests, pathogens and vegetation. Pitman, London.
- Johnston, R. L. & G. W. Bishop. 1987. Economic injury levels and economic thresholds for cereal aphids (Homoptera: Aphididae) on spring-planted wheat. J. Econ. Entomol., 80: 478–482.
- Kieckhefer, R. W., W. F. Lytle & W. Spuhler. 1974. Spring movement of cereal aphids into South Dakota. Environ. Entomol., 15: 567–572.
- Kiriak, I., F. Gruber, T. Poprawski, S. Halbert & L. Elberson. 1990. Occurrence of sexual morphs of Russian wheat aphid, *Diuraphis noxia* (Homoptera: Aphididae), in several locations in the Soviet Union and the northwestern United States. Proc. Entomol. Soc. Wash., 92: 544–547.
- Phillips, W. J. 1916. *Macrosiphum granarium*, the English grain aphid. J. Agr. Res., 7: 463–480.
- Pike, K. S. & R. L. Schaffner. 1985. Development of autumn populations of cereal aphids, *Rhopalosiphum padi* (L.) and *Schizaphis graminum* (Rondani) (Homoptera: Aphididae), and their effects on winter wheat in Washington State. J. Econ. Entomol., 78: 676–680.
- Rabbinge, R., E. M. Drees, M. van der Graaf, F. C. M. Verberne & A. Wesseki. 1981. Damage effects of cereal aphids in wheat. Neth. J. Pl. Path., 85: 197–220.
- Robinson, A. G. & S. Hsu. 1963. Host plant records and biology of aphids on cereal grains and grasses in Manitoba (Homoptera: Aphididae). Can. Entomol., 95: 134–137.
- Vickerman, G. P. & S. D. Wratten. 1979. The biology and pest status of cereal aphids (Homoptera: Aphididae) in Europe: a review. Bull. Ent. Res., 69: 1–32.

Received 3 July 1991; accepted 1 April 1992.